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Recovery of conservation values in Central African rain forest after logging and shifting cultivation

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Abstract. Secondary forests in Central Africa are increasing in importance for biodiversity conservation as old growth forests outside the few protected areas are disappearing rapidly. We examined vegetation recovery in a lowland rain forest area in Cameroon based on a detailed botanical survey of old growth forest and different-aged logging gaps (5–27 years) and shifting cultivation fields (10–60 years). Our analysis focuses on the long-term recovery of botanical conservation values by analysing trends in vegetation structure, species composition, species diversity and levels of endemism and rarity. In the total survey (4.25 ha), we recorded 834 species of which 23% were endemic to the Lower Guinea forest region. The proportion of endemic species was high in shrubs and low in herbs. Geographic range and (local) rarity were not significantly associated. The proportion of rare species (relative frequency $<10\%$) was high in woody climbers and low in trees. In logging gaps, recovery of all vegetation characteristics was relatively quick (5–14 years). Recovery in shifting cultivation sites took longer (30–60 years). Endemic species were found to be highly sensitive to shifting cultivation practices and even after 50–60 years the level of endemism was still significantly lower compared to old growth forest. The proportion of rare species was not significantly different between disturbed sites and old growth forest. We conclude that secondary forests can contribute to biodiversity conservation, e.g. as buffer zones around protected areas. However, this contribution should be assessed differently between land use types and widespread versus endemic species.

Introduction

Central and West African rain forests are estimated to hold 8000 plant species, of which 80% are endemic to the region (Sayer et al. 1992). Combined with substantial recent habitat loss, this has led to the classification of this forest region as one of the top 25 conservation priority areas of the world (Myers et al. 2000). Despite this importance, Central and West African rain forests are poorly protected. In West Africa some 20% of the remaining forest cover is protected, in Central Africa only 7% (Sayer et al. 1992). Outside protected areas, forest use such as logging, plantation agriculture and shifting cultivation has intensified during the last decades,

leading to large-scale forest degradation (Sayer et al. 1992). At present, research and conservation management tend to focus on undisturbed tropical forests while little attention is given to disturbed ecosystems. However, as relatively undisturbed ('old growth') forests are becoming scarce and fragmented in many tropical regions, secondary forests may become critical for future biodiversity conservation (Brown and Lugo 1990; Aide et al. 1995). To evaluate the role of secondary forests for biodiversity conservation, more insight is needed on the effects of human land use activities on forest composition, and especially conservation values.

Species diversity, levels of endemism and rarity, naturalness and exposure to threats are generally accepted as a robust set of criteria for setting conservation priorities (de Groot 1992; Hawthorne 1996). However, current evaluations of conservation values in tropical rain forests only use present-day characteristics of forest communities, while overlooking future potentials of recovery through secondary succession. Examples are the 'silver bullet' strategy for global conservation priorities proposed by Myers et al. (2000) and the identification of an optimal reserve network for biodiversity conservation in Uganda proposed by Howard et al. (2000). These static approaches may work for relatively stable old growth forests, but are unsuitable for highly dynamic secondary forests. On the other hand, existing studies of tropical forest succession characterise forest dynamics but often do not evaluate characteristics important to conservation (e.g. de Rouw 1991; Aide et al. 2000; Peña-Claros 2001).

Conservation values should ideally be assessed using different trophic and functional groups of organisms (Howard et al. 1998; Lawton et al. 1998). However, logistic problems and insufficient taxonomic knowledge make relatively rapid surveys of especially small-sized animal groups impossible in most tropical regions. Being taxonomically relatively well studied, plants are therefore often used as a proxy variable for conservation evaluations (Zonneveld 1995). Most plant regeneration studies of tropical forests focus on trees (e.g. Swaine and Hall 1983; Saldarriaga et al. 1988; Peña-Claros 2001; Slik et al. 2002). This may, however, underestimate the conservation value of an area. For instance, some 67% of the endangered and rare forest plant species of West Africa are non-trees (J.J. Wieringa, personal communication). Conservation evaluations using plants should therefore be based on as many growth forms, functional types and taxonomic groups as possible (Lawton et al. 1998).

The recovery potential of secondary forests is strongly influenced by the size and intensity of disturbances. In natural forests, advanced regeneration, sprouting and the seed bank are relatively important in filling small canopy gaps, while light-demanding immigrants constitute the majority of plants filling large gaps (Bazaz 1991; Whitmore 1991). Anthropogenic disturbances like logging and forest clearing for agriculture are generally more severe than natural gap phase dynamics and therefore regeneration will be determined by long-range dispersers (Uhl et al. 1981; Nepstad et al. 1996; Wijdeven and Kuzee 2000). Many of these pioneer species are of limited concern to conservation, as they generally have large distribution ranges and are little site-specific (Ewel 1980). Therefore, studies that address the conservation value of secondary forest should extend beyond the pioneer stages of succes-

sion. However, current regeneration studies in West and Central Africa are restricted to the first 5–10 years (e.g. Aweto 1981; Swaine and Hall 1983).

In this study we analyse the recovery of lowland rain forest in South Cameroon following the two most widespread land uses in the region: logging and shifting cultivation. We conducted a detailed botanical survey, including all major terrestrial growth forms, of logging gaps of 5–27 years old and shifting cultivation fields of 10–60 years old. We evaluate the long-term recovery of vegetation characteristics and conservation values by analysing trends in vegetation structure, species composition, species diversity, and levels of endemism and rarity.

Methods

Research area

The study was conducted in the Bipindi–Akom II–Lolodorf region, south Cameroon (3° N, 10° E). The climate is humid tropical with two distinct wet seasons (March–May and August–November) and two relatively dry periods. The average annual rainfall is 2000 mm (Waterloo et al. 2000). Average monthly temperatures vary between 22.9 and 27.5 °C (Olivry 1986). The parent material consists of Precambrian metamorphic rocks and old volcanic intrusions (Franqueville 1973). Topography varies from flat erosional plains to rolling uplands with isolated hills. Altitude varies from 50 to 600 m a.s.l. Soils range from moderately acid sandy clay loam to highly clayey and strongly acid and classify as Haplic Acrisols, and Plinthic and Xanthic Ferrasols (van Gemerden and Hazeu 1999). Evergreen forests of the Atlantic Biafrian type largely cover the area (Letouzey 1968, 1985). These forests are characteristically rich in Leguminosae–Caesalpinioideae and have a closed canopy at 30–40 m with emergents often surpassing 55 m.

The area is sparsely populated (8.6 persons/km^2) and population increase is marginal (+0.4%; Lescuyer et al. 1999). Most people practice shifting cultivation, a form of agriculture in which forest patches of 0.5–1.0 ha are cleared, burned and interplanted with a variety of crops. Depending on soil productivity, the tending and harvesting gradually stops after 2–3 years and the land is left fallow for at least 7–15 years (Nounamo and Yemefack 2002). Shifting cultivation is confined to the direct surrounding of villages and along the main access roads (van Gemerden and Hazeu 1999).

The main economic activity in the area is timber exploitation. Most of the area has been selectively logged, and some parts twice, by international logging companies. The logging involves the use of heavy machinery for road construction and log extraction. Present logging activities focus on *Lophira alata* Banks ex Gaertn. f. (Ochnaceae; commercial name Azobé; 60% of the extracted volume), *Erythrophleum ivorense* A. Chev. (Leg.-Caesalpinioideae; Tali), and *Pterocarpus soyauxii* Taub. (Leg.-Papilionideae; Padouk). The logging intensity is low (10 m^3/ha or 0.7 tree/ha). The felling and extraction of logs causes physical damage to 5% of the area but locally much higher (25%) disturbance rates have been observed (Jonkers and

Table 1. Vegetation characteristics and distribution of 25 × 25 m plots by land use and age classes.

Land use	Old growth	Logging			Shifting cultivation		
Vegetation age (years)	–	5	14	27	10–20	30–40	50–60
Canopy height (m)[a]	26	20	28	27	22	21	25
Tree density (stems per ha)[a]							
dbh ≥ 10 cm	639	435	384	379	365	435	400
dbh ≥ 30 cm	117	80	96	77	93	67	85
# plots (625 m^2)	20	10	7	8	7	5	11
Surveyed area (ha)	1.25	0.63	0.44	0.50	0.44	0.31	0.69
Research sites[b]	ABCD	CD	AB	AB	C	C	C

[a]Means based on a random set of three plots extended to 25 × 50 m (1250 m^2) per land use/age category, except for old growth (six plots) and logging 14 years (two plots). [b]A = Bibindi area (3°00′ N, 10°24′ E, altitude 120–300 m), B = Ebimimbang area (3°02′ N, 10°26′ E, 50–180 m), C = Ebom area (3°03′ N, 10°43′ E, 400–450 m), D = Minwo area (3°05′ N, 10°45′ E, 480–600 m).

van Leersum 2000). Individual crown fall gaps caused by commercial logging are between 300 and 900 m^2 (Parren and Bongers 2001), but simultaneous felling of clumps of commercially interesting trees often creates much larger gaps (B.v.G., personal observation).

Survey plots

Vegetation in gaps of 5, 14 and 27 years after logging, and in shifting cultivation fields of 10–20, 30–40, and 50–60 years since tending of fields has stopped, was sampled by plots of 25 × 25 m (625 m^2). A total of 68 plots were sampled, i.e. 4.25 ha. Plots were selected in homogenous and representative vegetation following a reconnaissance scale vegetation survey of the area (van Gemerden and Hazeu 1999). Secondary vegetation was found to be very similar throughout the area and therefore shifting cultivation plots were clustered in one research site where reliable information on historical agricultural use was available. Logging plots were located in four research sites to increase the span of the studied chronosequence (Table 1). The maximum distance between sites was less than 40 km and land use practices were comparable. In all four localities old growth forest was sampled.

Land use history was determined with the help of local informants, often the proprietors of the sites. Information on logging activities in the area was also provided by the state forestry service ONADEF (Hazeu et al. 2000). Plots in logging gaps were positioned in the estimated centre of the tree crown fall. Most exploited trees are *Lophira alata*, a species with extremely hard wood, and branches and bole are, even after 27 years, clearly visible. Plots in fallow vegetation were positioned well away from sudden changes in vegetation structure or other anomalies. Within-plot variation in topography, vegetation and drainage characteristics was minimal.

Survey methods

All individuals of terrestrial higher plants (all growth forms) were recorded per plot. Only woody plants with heights less than 50 cm were not sampled because of

foreseen identification problems. Species and size class of each individual was recorded. Within each growth form category, individuals were assigned to the following size classes: total height (h) <50 cm (non-woody species only), $h \geq 50$ cm and diameter at breast height (dbh) <2 cm, dbh 2–4.9, 5–9.9, 10–19.9, etc. We considered all apparent solitary ramets as individuals. Each tussock of herbs was counted as an individual. Diameters of stems of multi-stemmed shrubs were summed.

Plant species identification

In the field, the most common and readily identifiable species were directly named and plant material was collected of all other species. A total of nearly 11 000 vouchers were collected in the survey. The vouchers were processed at the Kribi Herbarium (Tropenbos Cameroon Herbarium) and sent to the National Herbarium of Cameroon in Yaounde and the Nationaal Herbarium Nederland (Wageningen University Branch) for identification by specialists. Unidentified species were categorised as morphospecies. Ferns and fern allies were collected but have not been identified. Nomenclature follows Lebrun et al. (1991–1997).

Species' growth form and geographical distribution were identified on the basis of taxonomic literature, mainly Cable and Cheek (1998), Aubréville and Leroy (1961–1992, 1963–2001), Keay and Hepper (1954–1972), and own field observations. Growth form classification largely followed Cable and Cheek (1998), and species were classified as trees (single-stemmed, maximum height at least 3 m; generally much taller), shrubs (multi-stemmed or <3 m tall), woody climbers (including rattans), non-woody climbers, herbs (terrestrial), hemi-epiphytes, palms or stranglers. Categories used to classify species' geographical distribution range reflect general patterns of biogeography. However, as large parts of West and Central Africa have only been poorly explored botanically, available information was generally too imprecise to assess species distribution patterns at smaller than regional scales. Therefore, species were classified as Lower Guinea endemics (species restricted to the forest region of Nigeria, Cameroon, Equatorial Guinea and Gabon), Guineo–Congolian species (species restricted to the Senegal–Gabon–Zaire forest region), and Paleo and pan tropical species (species widely distributed in Africa). Each species was assigned to the geographic range category that included the complete distribution range.

Data analysis

Analysis of variance (ANOVA) was used to compare plant density, basal area, species richness, and species diversity between vegetation ages and land use types. We compared disturbed sites with old growth forests using a Tukey test ($P < 0.05$). Species diversity was expressed as the Shannon diversity index H' (see Magurran 1988). Plant density and basal area were calculated using all individuals encountered in the plots. Species richness and species diversity were calculated using

individuals that were at least morphocategorised. As a result, our richness and diversity estimates are likely to be conservative.

To assess recovery in terms of species composition, we calculated the similarity of disturbed sites with each of the old growth sites ($n = 20$). Average similarity with old growth plots was used to compare recovery of species composition between disturbed sites (ANOVA followed by Tukey tests, $P < 0.05$). Both qualitative and quantitative similarity was calculated using the Sörenson index, expressing for two samples which proportion of all observed species they have in common (see Magurran 1988). Qualitative similarity was based on presence/absence data of species per plot. Quantitative similarity was based on the log transformed relative species abundance. Only individuals that are at least morphocategorised were included in the analyses.

Species rarity is a measure for the local distribution of species. Rare species have a higher risk of (local) extinction under unfavourable conditions (Rosenzweig 1995). Species rarity was calculated as the relative frequency of occurrence in 68 plots. Species were classified as rare (occurring in less than 10% of the plots), intermediate (10–60% plots) and common (≥60% plots). Association of rarity and geographic range was analysed with a Kruskal–Wallis test ($P < 0.05$), based on species' actual relative frequency. Association of rarity classes and growth form and of geographic range and growth form was tested with a χ^2 ($P < 0.05$).

Results

Floristic characteristics

We recorded a total of 63 384 individual plants (including ferns and fern allies) in 4.25 ha. Of all individual plants, 74% were identified to species level, and 10% were categorised as morphospecies. Only 3 and 4% remained undetermined at the genus level and family level, respectively. Finally, 9% of the plants were assigned to a field identification that turned out to represent a small number of morphologically similar (botanical) species. Such clusters were treated in the analyses as a single species. In total, 59 529 individual plants representing 94% of all individuals were at least morphocategorised and used in the analyses. The proportion of unidentified plants varied among the different land use/age categories ($F_{6,61} = 2.76$, $P = 0.019$, no Tukey subsets). The mean proportion of unidentified plants ranged from 2.2% in shifting cultivation fields of 30–40 years to 5.8% in old growth forest. We do not expect that these small differences will affect the overall outcome of the analyses. In the survey, we found a total of 834 species belonging to 359 genera and 90 families. Predominant families encountered were Rubiaceae (140 species), Euphorbiaceae (53), Apocynaceae (39), Leguminosae-Caesalpinioideae (34), Annonaceae (31) and Ebenaceae (27).

Rare species (species occurring in less than 10% of the plots) accounted for 63% of all species but represented only 6% of the individuals. Less than 7% of the species occurred in more than 60% of the plots. These 'common' species accounted for 53%

Table 2. Mean relative abundance and relative frequency of the most abundant species per growth form in old growth forest, logging gaps and shifting cultivation fields.

Family	Species[a,b]	Mean relative abundance[c,d]			Relative frequency[c,e]		
		OG	L	SC	OG	L	SC
Trees (345 species)							
Sterculiaceae	*Scaphopetalum blackii* Mast.	7.1	2.9	3.1	IV	III	V
Moraceae	*Treculia obovoidea* N.E. Br.	6.3	1.7	0.8	V	IV	V
Icacinaceae	*Lasianthera africana* P. Beauv.	3.5	6.0	3.0	V	V	V
Shrubs (151 species)							
Euphorbiaceae	*Manniophyton africanum* Müll. Arg.	22.9	9.5	0.2	III	III	I
Sterculiaceae	*Scaphopetalum thonneri* Willd.	18.1	19.1	18.7	III	IV	III
Euphorbiaceae	*Alchornea floribunda* Müll. Arg.	4.1	4.1	12.9	IV	IV	V
Monimiaceae	*Glossocalyx brevipes* Benth.	3.5	6.1	3.4	III	II	IV
Rubiaceae	*Chazaliella sciadephora* (Hiern) Petit and Verdc.	2.7	1.4	10.4	II	II	IV
Dracaenaceae	*Dracaena bicolor* Hook.	1.8	10.2	0.1	I	III	+
Rubiaceae	*Chazaliella domatiicola* (De Wild.) Petit and Verdc.	0.1	0.1	8.2	+	r	IV
Woody climbers (150 species)							
Marantaceae	*Haumania danckelmaniana* (J. Braun and K. Schum.) Milne-Redh.	49.2	54.4	57.5	V	V	V
Palmae	*Eremospatha cf. wendlandiana* Dammer ex Becc.	8.7	7.1	4.9	V	V	V
Connaraceae	*Agelaea pentagyna* (Lam.) Baill.	6.9	4.8	6.1	V	IV	IV
Icacinaceae	*Lavigeria macrocarpa* (Oliv.) Pierre	4.2	6.4	4.3	IV	IV	V
Palmae	*Laccosperma secundiflorum* (P. Beauv.) Kuntze	0.8	2.8	8.1	II	II	IV
Non-woody climbers (37 species)							
Araceae	*Cercestis congensis* Engl.	48.4	34.6	55.2	V	V	V
Araceae	*Cercestis mirabilis* (N.E. Br.) Bogner	29.9	50.3	38.5	V	V	V
Araceae	*Culcasia obliquifolia* Engl.	13.7	2.5	0.0	II	I	−
Vitaceae	*Cissus barteri* (Baker) Planch.	0.5	5.1	0.7	I	II	II
Herbs (72 species)							
Gramineae	*Leptaspis zeylanica* Nees	27.6	9.7	1.0	V	V	III
Gramineae	*Microcalamus barbinodis* Franch.	14.8	4.1	6.8	II	II	II
Marantaceae	*Trachyphrynium braunian* (K. Schum.) Baker	5.0	13.1	4.8	III	V	V
Araceae	*Stylochaeton zenkeri* Engl.	3.0	3.5	15.4	III	III	V
Marantaceae	*Sarcophrynium cf. Prionogonium* (K. Schum.) K. Schum.	2.6	8.8	4.5	II	IV	III
Commelinaceae	*Palisota ambigua* (P. Beauv.) C.B. Clarke	1.7	11.6	4.0	III	V	V
Marantaceae	*Megaphrynium macrostachyum* (Benth.) Milne-Redh.	1.1	9.3	20.2	I	V	V
Marantaceae	*Thaumatococcus daniellii* (Benn.) Benth.	0.5	4.9	15.6	+	I	IV

[a]Growth form was identified for 765 species (92% all species, 95% all individuals). [b]Species with mean relative abundance ≥5% in at least one land use category. [c]Land use categories: OG = old growth forest (n = 20); L = logging gaps (n = 25), SC = shifting cultivation fields (n = 23). [d]Mean relative abundance is the average proportion of individuals per growth form per plot. [e]Species relative frequency is the proportion of plots per land use category in which the species was present. Frequency classes: − = not present; r = <5% plots; + = 5–10%; I = 10–20%; II = 20–40%; III = 40–60%; IV = 60–80%; V = 80–100%.

of all individuals. Only one species, *Haumania danckelmaniana* (J. Braun and K. Schum.) Milne-Redh. (Marantaceae), was found in all plots. Woody climbers, non-woody climbers and herbs were dominated by a small number of species, while only three tree species had average relative abundance larger than 5% (Table 2).

We assigned 765 species (92% of species, 95% of individuals) to growth forms. The most species-rich growth forms were trees, woody climbers and shrubs (Table

Table 3. Distribution of species and rarity by geographic range of the most important growth forms.

Growth form	Trees			Shrubs			Woody climbers			Non-woody climbers			Herbs			All growth forms		
Geographic range[a,b]	# spp	% spp	Rarity[c]	# spp	% spp	Rarity[c]	# spp	% spp	Rarity[c]	# spp	% spp	Rarity[c]	# spp	% spp	Rarity[c]	# spp	% spp	Rarity[c]
Lower Guinea	53	22.3	7.7	27	40.9	4.6	17	20.2	14.9	2	12.5	10.0	4	10.8	3.1	104	23.3	6.2
Guinea–Congolia	125	52.5	15.4	28	42.4	6.2	57	67.9	10.4	10	62.5	7.0	21	56.8	12.3	245	54.8	9.2
Paleo and pan tropical	60	25.2	13.1	11	16.7	7.7	10	11.9	14.0	4	25.0	10.0	12	32.4	10.0	98	21.9	11.6

[a] Geographic range and growth form was identified for 447 species (54% of all species). [b] Lower Guinea = species endemic to Nigeria, Cameroon, Equatorial Guinea and Gabon; Guinea–Congolia = species restricted to the Senegal–Gabon–Zaire forest region (Lower Guinea endemics not included); Paleo and pan tropical = species occurring throughout Africa (excluding Lower Guinean and Guinea–Congolian species). [c] Rarity is expressed as median of relative frequencies of species over 68 plots. Rarity per growth form did not differ significantly between geographic ranges (Kruskal–Wallis tests, trees: $\chi^2_2 = 5.05$, $P = 0.08$; shrubs: $\chi^2_2 = 0.65$, $P = 0.723$; woody climbers: $\chi^2_2 = 0.71$, $P = 0.707$; non-woody climbers: $\chi^2_2 = 0.03$, $P = 0.987$; herbs: $\chi^2_2 = 1.93$, $P = 0.382$; all growth forms: $\chi^2_2 = 4.41$, $P = 0.110$).

Table 4. Species rarity, geographic range composition and species and plant density of the most important growth forms in old growth forest, logging gaps and shifting cultivation fields.

Growth form	Trees			Shrubs			Woody climbers			Non-woody climbers			Herbs			All growth forms		
Land use[1]	OG	L	SC	OG	L	SC	OG	L	SC	OG	L	SC	OG	L	SC	OG	L	SC
Species rarity[2,3,4]																		
Rare species (<10% plots)	2.5	2.8	3.6	12.8	13.4	18.0	13.3	14.3	10.0	8.6	17.0	18.0	8.5	7.5	7.0	14.8	15.2	13.3
	1.0	1.9	1.4	4.8	7.4	8.3	3.8^{b}	$2.8^{a,b}$	1.5^{a}	4.6	2.2	2.8	4.6	1.1	2.5	7.8	4.8	5.1
Common species (≥60% plots)	33.4	33.0	33.4	14.7	16.0	14.6	31.9	25.9	27.7	51.7	49.9	54.1	46.3	44.9	44.3	30.3	30.0	30.1
	47.5	46.6	51.5	28.0	29.2	34.7	73.9	75.6	75.7	78.4	84.9	93.6	46.2	53.2	53.8	49.3	53.8	56.4
Species geographic range[2,4,5,6]																		
Lower Guinea (endemics)	21.6^{b}	14.8^{a}	13.1^{a}	38.8^{a}	48.9^{b}	30.4^{a}	38.1^{b}	24.9^{a}	24.3^{a}	15.1^{b}	7.6^{a}	0^{a}	0.6	2.1	1.8	23.7^{c}	18.9^{b}	14.5^{a}
	18.6^{b}	$13.8^{a,b}$	11.2^{a}	23.4^{a}	40.8^{b}	15.7^{b}	74.1	70.2	69.4	14.8^{b}	2.5^{a}	0^{a}	0.3	0.4	0.2	22.9^{b}	$19.4^{a,b}$	14.4^{a}
Guinea–Congolia	$63.9^{a,b}$	64.7^{b}	60.0^{a}	30.5^{b}	19.6^{a}	49.0^{c}	47.4^{a}	59.6^{b}	61.4^{b}	82.8	81.0	89.4	81.1^{b}	63.3^{a}	59.6^{a}	60.0	59.2	59.9
	62.6^{a}	71.9^{b}	$64.8^{a,b}$	15.3^{a}	11.3^{a}	53.6^{b}	14.8	22.2	21.9	85.7^{a}	$96.2^{a,b}$	98.2^{b}	87.0^{b}	62.5^{a}	62.4^{a}	53.5	57.4	58.4
Paleo and pan tropical	14.6^{a}	20.1^{b}	26.9^{c}	30.7^{b}	31.4^{b}	20.6^{a}	14.4	15.5	14.3	3.1	11.4	11.1	18.3^{a}	34.6^{b}	38.7^{b}	16.3^{a}	21.9^{b}	25.6^{c}
	$18.4^{a,b}$	14.7^{a}	24.0^{b}	61.2^{c}	$47.9^{a,b}$	30.7^{a}	11.2	7.6	8.7	0.3	1.3	1.9	12.7^{a}	37.1^{b}	37.4^{b}	23.6	23.2	27.2
Species and plant density[2,5]																		
Mean # species per 625 m^2	68.2	69.3	70.1	17.2	17.3	17.9	14.2	16.3	16.0	4.0	4.4	4.0	8.0^{a}	12.1^{b}	14.4^{b}	116.7	123.5	128.5
Mean # individuals per ha	4626	3934	4131	1803	1442	1906	1286^{a}	1317^{a}	2453^{b}	787^{a}	923^{a}	1626^{b}	2661^{a}	3747^{a}	8634^{b}	12004^{a}	12234^{a}	20152^{b}

[1] OG = old growth forest (n = 20); L = logging gaps (n = 25); SC = shifting cultivation fields (n = 23). Plot size is 625 m^2. [2] Species rarity and species and plant density are based on 834 species (the growth form of 765 species was identified). Geographic range composition is based on 447 species (53.6% total species and 77.4% total individuals). [3] Species rarity is expressed as relative frequency of species over 68 plots. Rare species are species with relative frequency <10%. Common species are species with relative frequency ≥60%. [4] Mean proportions of species (upper line) and individuals (lower line) per growth form and land use category. [5] Values with the same letter are not significantly different between land use categories (Tukey test after analysis of variance, $P < 0.05$). [6] Lower Guinea = species endemic to Nigeria, Cameroon, Equatorial Guinea and Gabon; Guinea–Congolia = species restricted to the Senegal–Gabon–Zaire forest region (Lower Guinea endemics not included); Paleo and pan tropical = species occurring throughout Africa (excluding Lower Guinean and Guinea–Congolian species).

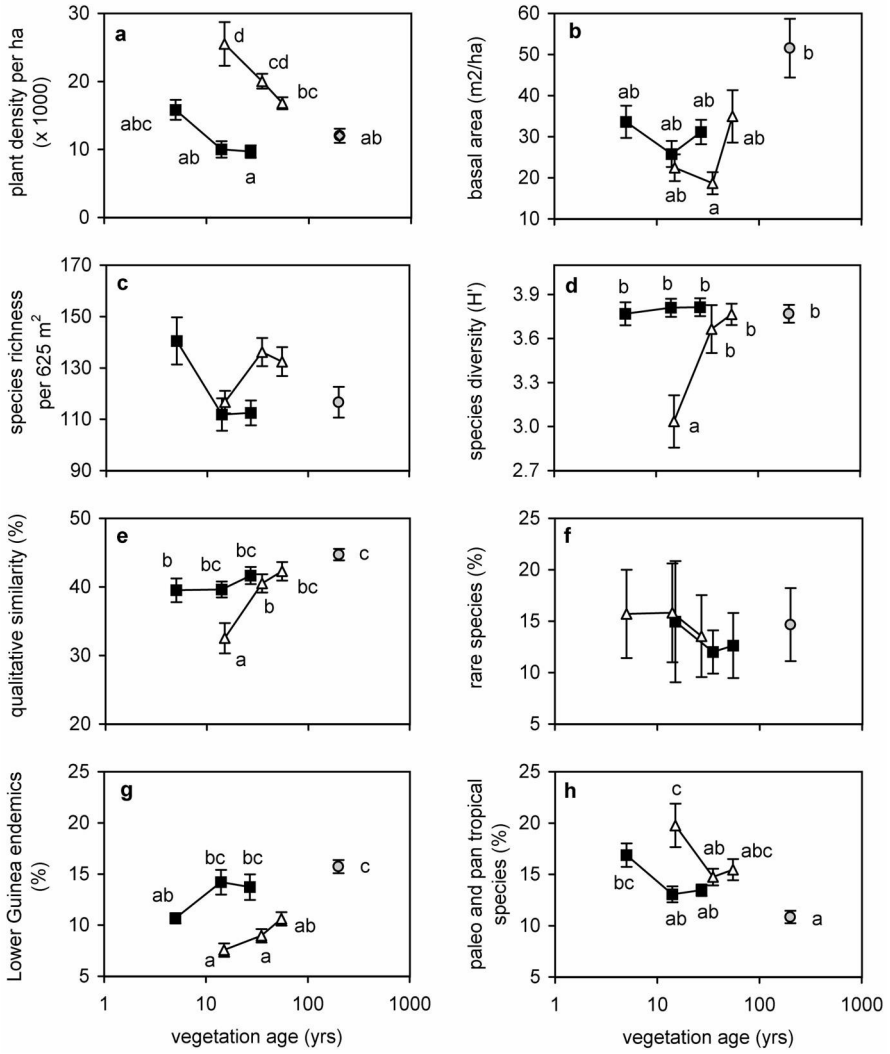

Figure 1. Recovery of different vegetation characteristics after selective logging (filled squares) and shifting cultivation (open triangles) as compared to old growth forest (shaded circles). Values represent means ± standard errors. Means with the same letter are not significantly different (Tukey test after ANOVA, $P < 0.05$).

2). Together they represent nearly 85% of the species and 54% of the individuals. The geographical distribution range was identified for 447 species (54% of species, 73% of individuals). Of these species, 22% had paleo and pan tropical ranges. At the other extreme, more than 23% of the species were endemic to the Lower Guinea forest region (South Nigeria–Gabon). This category included 4% of the species that, according to available taxonomic literature, were strictly confined to Cameroon.

Geographic distribution range and growth form were significantly associated ($\chi^2_8 = 25.13$, $P = 0.01$). The proportion of endemics was highest in shrubs (41%) and lowest in herbs (11%). Species rarity did not differ significantly among distribution ranges (Kruskal–Wallis tests, $P > 0.05$; Table 3). Growth form and rarity classes were significantly associated ($\chi^2_8 = 41.45$, $P < 0.001$). The proportion of rare species was high in woody climbers (73%) and shrubs (70%), and low in trees (49%).

Recovery of forest structure

The number of individual plants per plot ranged from 326 to 2616 (average 928, i.e. 14 848 ha^{-1}). The average number of individuals per plot varied among growth forms and land use categories (Table 4). The most abundant growth forms were herbs (mean 337 individuals per plot), trees (263), shrubs (107), woody climbers (106), and non-woody climbers (70).

Herbs were significantly more abundant in shifting cultivation sites of 10–20 years compared to old growth forest ($F_{6,61} = 14.53$, $P < 0.001$). The large number of herbs found in these sites accounted largely for the differences in total plant densities (Figure 1a; $F_{6,61} = 12.36$, $P < 0.001$). Furthermore, shifting cultivation sites of 10–20 and 30–40 years had a much larger number of individuals with $h \geq 50$ and dbh < 2 cm ($F_{6,61} = 10.52$, $P < 0.001$). Other size classes showed no significant trend among land use/age categories. Climbers, both woody and non-woody, reacted differently to logging and shifting cultivation practices. With vegetation age, densities of non-woody climbers ($F_{6,61} = 4.33$, $P = 0.001$) and woody climbers ($F_{6,61} = 5.26$, $P < 0.001$) increased in shifting cultivation sites and remained constant in logging sites. Both growth forms were significantly more abundant in 30–40 year old shifting cultivation sites compared to old growth forest. Densities of trees and shrubs were not affected by disturbance (Table 4).

Basal areas ranged from 0.64–5.89 m^2 per plot (dbh ≥ 2 cm, average 2.13 m^2, i.e. 35.76 m^2/ha). The general trend in both logging and shifting cultivation sites was that the basal area was lower at intermediate age compared to younger and older stands (Figure 1b). Variation within land use/age categories was, however, considerable; only shifting cultivation sites of 30–40 years had a significant lower basal area than old growth forest ($F_{6,61} = 3.40$, $P = 0.006$).

Recovery of species richness, diversity and composition

Species richness (# species per plot) ranged from 75 to 173 (average 123) and varied with growth form and land use (Table 4). The most species rich growth forms were trees (mean 69 species per plot), followed by shrubs (17), woody climbers (16), and herbs (13). With vegetation age, overall species richness decreased in logging sites and increased in shifting cultivation sites ($F_{6,61} = 2.72$, $P = 0.021$, Figure 1c). Trees, on average the most species rich growth form per plot, were largely responsible for the general trend ($F_{6,61} = 2.77$, $P = 0.019$). Herb species richness was, compared to old growth forest, higher in 5-year old logging sites and

shifting cultivation sites of 30–40 years ($F_{6,61} = 6.73$, $P < 0.001$). Species richness of the other growth forms showed no clear trend. The Shannon diversity of the vegetation ranged from 2.3 to 4.3 (average 3.7). Five-year old logging sites already had Shannon diversity values comparable to those of old growth forest, while shifting cultivation sites of 10–20 years still had significantly lower values ($F_{6,61} = 7.35$, $P < 0.001$, Figure 1d).

The average qualitative (presence/absence) similarity between old growth plots varied from 40 to 47%. The mean qualitative similarity of disturbed sites to old growth vegetation increased with vegetation age ($F_{6,61} = 12.35$, $P < 0.001$; Figure 1e). Logging sites reached qualitative similarity values comparable to old growth forests after 14 years, whereas such values were only reached in shifting cultivation sites after 50–60 years. Mean quantitative similarity (log transformed relative abundance) of disturbed plots and old growth forest was generally lower than qualitative similarity and ranged from 16 to 34%. However, variation was high and no significant relation between quantitative similarity, land use and vegetation age was found. Quantitative similarity based only on woody species did not show a significant relation either.

Recovery of rare and endemic species

The proportion rare species (<10% plots) ranged from 6 to 14% and showed high variation within land use categories. Per growth form and for all species, the proportion of rare and common species (≥60% plots) did not differ significantly between old growth forest and disturbed sites (Figure 1f; Table 4).

The level of endemism was strongly influenced by land use (Table 4). The proportion of species endemic to Lower Guinea (Nigeria–Gabon) increased with vegetation age ($F_{6,61} = 13.81$, $P < 0.001$; Figure 1g). The proportion of species with large ranges decreased with vegetation age (Paleo–pan tropical; $F_{6,61} = 9.01$, $P < 0.001$; Figure 1h). The geographic range composition of logging sites was not significantly different from old growth forests, except for Paleo–pan tropical species and Lower Guinea endemics in 5-year old sites. Shifting cultivation sites recovered much slower and attained old growth values in 30–40 years for the Paleo–pan tropical species. Even after 50–60 years, the proportion of Lower Guinea endemics was still significantly lower in shifting cultivation sites compared to old growth forest.

Discussion

Vegetation recovery

The results show that most forest characteristics of rain forest in Cameroon recovered from selective logging and shifting cultivation. After 27 years logged sites strongly resembled old growth forest sites. In shifting cultivation sites, recovery was generally slower but after 50–60 years sites attained old growth values for most forest characteristics. However, even after 50–60 years the proportion of

endemic species was still significantly lower in shifting cultivation sites compared to old growth forests. Changes in species composition, species richness and species diversity suggest that the mechanism of vegetation recovery is different in logging gaps and shifting cultivation areas (Figure 1). Species richness in logging gaps was initially high, but decreased with vegetation age and was similar to old growth forests after 14 years. Logging sites were also floristically similar to old growth forests after 14 years. This indicates that regeneration in logging sites was largely made up of species of the surrounding forest pool and the observed early reduction in species number appears to be at the cost of invading pioneer species. In shifting cultivation areas, pioneer species appear to dominate succession much longer. Species richness in these sites was initially similar to that of old growth forests, but floristically they were very different. With time, species diversity and floristic similarity increased and old growth values were attained after 30–40 and 50–60 years, respectively.

Logging and shifting cultivation practices probably influence regeneration differently as a result of differences in use intensity, rate of recurrence and species selectivity of the disturbance (e.g. removal of few large individuals of selected tree species or removal of all plants; Brown and Lugo 1990). In logging gaps, mass destruction of dominant vegetation cover occurs but generally many seedlings and saplings survive the crown fall (Whitmore 1991). Furthermore, resprouting is common among forest species and contributes considerably to the filling of canopy gaps (Uhl et al. 1981; Bazaz 1991; Parren and Bongers 2001). As a consequence, regeneration in most logging sites is formed by individuals that were already present before disturbance. In shifting cultivation sites, vegetation removal, burning, soil disturbance and weeding effectively eliminate possibilities for advance regeneration and resprouting and cause a depletion of the original forest seed bank (Uhl et al. 1981, 1988; Wijdeven and Kuzee 2000). Wijdeven and Kuzee (2000) found forest recovery in pastures to be strongly limited by the availability of seeds. The species that are successful in reaching open pasture sites and capable of avoiding seed and seedling predation were generally pioneer species. Although pastures are generally more intensively disturbed, the same mechanism seems to apply to shifting cultivation sites.

Compared to other tropical forests, recovery of basal area, plant densities and species composition was relatively fast in Cameroon. Basal area and plant density recovered in 5 years in logged areas and in 50–60 years in shifting cultivation sites. In Uganda, structural recovery following selective logging took more than 50 years (Plumptre 1996), while areas used for shifting cultivation in the Amazon region were estimated to need 200 years (Saldarriaga et al. 1988). We found that floristic recovery took 14 years in logged sites and 50–60 years in shifting cultivation sites. Floristic recovery in other regions ranged from 40 to 200 years (Kappelle et al. 1995; Kurpick et al. 1997; Aide et al. 2000) and is likely to be strongly influenced by the landscape context (Liu and Ashton 1999). Fast recovery of especially floristic composition after disturbance indicates that the old growth forests in this study contain a large set of species capable of colonising disturbed sites. As shifting cultivation sites are larger and much more intensively used than natural gaps, the species capable of colonising such sites are likely to be outcompeted in relatively

stable forests with gap-phase dynamics as the main disturbance regime. Therefore, our results suggest that the history of the current old growth forests may have included large-scale disturbances. To explain the poor regeneration in canopy gaps of the currently dominating species *Lophira alata* and *Sacoglottis gabonensis* (Baill.) Urb. (Humeriaceae), Letouzey (1968) suggested that forests in large parts of the coastal zone of Cameroon have been cleared in the past for agriculture. An analysis of the complete old growth forest tree species composition in relation to recruitment preference also concludes that the forests in the study area were once subject to large-scale disturbances (B.S. van Gemerden, unpublished data). Long-term higher dynamics therefore appear to increase the speed and rate of recovery after disturbance.

Recovery of conservation values

The main focus of this study was the long-term effect of land use on botanical conservation values of tropical forests. Species diversity, rarity and endemism, naturalness and exposure to threats are generally accepted criteria for the assessment of conservation values (de Groot 1992; Hawthorne 1996; Howard et al. 2000; Myers et al. 2000). It should be noted that a clear preference for undisturbed ecosystems is embedded in these criteria. However, the future of tropical biodiversity conservation may largely depend on the management of disturbed areas (Brown and Lugo 1990). Too much focus on present-day values of species diversity, rarity and endemism of highly dynamic disturbed forests may overlook the potential of restoration through secondary succession.

In our survey, species diversity recovered quickly after disturbance. We found that after 5 years species diversity was restored in logged sites and after 30–40 years in shifting cultivation sites. This is comparable to the results for logged sites in Borneo (Cannon et al. 1998) and shifting cultivation sites in Bolivia (Peña-Claros 2001). Species richness tended to increase following disturbance, most likely due to an influx of secondary species. For interpretation of the conservation value of secondary forests, species diversity appears to be a more robust characteristic than species richness.

We found that many species in our survey occurred infrequently in the plots; 63% of the species occurred in less than 10% of the plots (rare species). Woody climbers and herbs had relatively many of such rare species, while trees had few. The proportion of rare species was highly variable between land use/age categories and no general pattern was found. Decreasing the cut-off level for rare species to 5% or increasing it to 20% of the plots did not influence this outcome. Individual rare species have a higher risk of local extinction under unfavourable conditions, as source populations are few and generally far apart (Rosenzweig 1995). Therefore, the level of rarity is of interest to biodiversity conservation. However, in the present survey, disturbed and undisturbed sites harboured sets of rare species and the conditions that would eventually lead to their extinction seem to vary. Thus, we conclude that the rarity criterion is difficult to interpret in terms of recovery of conservation values for the tropical secondary forest we studied.

Species endemic to Lower Guinea recovered relatively quickly in logging sites. After only 14 years the proportion of endemic species was comparable to that in old growth forest. Endemics did not recover in shifting cultivation areas in the 60 year covered in our study (Figure 1g). The proportion of species with large distribution ranges was initially higher in disturbed sites and recovery took respectively 14 and 30–40 years for logging and shifting cultivation sites (Figure 1h). This matches the observation of Aide et al. (2000) that dominant species colonising abandoned pastures in Puerto Rico were species with large geographical and altitude ranges.

Possible explanations for the slow recovery of endemics on shifting cultivation fields are (1) poor intrinsic dispersal ability, (2) low abundance of propagule sources, and (3) decline of pollination and dispersal vectors. No comprehensive studies are available on dispersal ability and pollination and dispersal vectors of African rain forest species. Poorter et al. (2001) examined growth form, shade tolerance, and morphological traits, such as fruit type, seed length and dispersal syndrome, of the rare and endemic species of West Africa. They found that epiphytes and shrubs had smaller distribution ranges than herbs, trees and lianas. Likewise, our results show that the proportion of endemic species was highest in shrubs and lowest in herbs and non-woody climbers (Table 3). Poorter et al. (2001) found no clear relations between distribution range and morphological traits. This suggests that wide-ranging species and narrow endemics have in general similar functional responses to the environment. The spatial distribution and local abundance of propagule sources could alternatively explain the poor recovery of endemic species in shifting cultivation sites. However, we found that local rarity (expressed as relative frequency) was not significantly associated with geographic distribution range. As endemic and non-endemic species have similar relative frequencies, the availability of propagule sources does not appear to explain their poor recovery in shifting cultivation fields. Finally, pollination and dispersal vectors may be negatively influenced by disturbance. The main seed vectors for open areas are birds and bats (Uhl et al. 1981). These animals are capable of dispersing the small, lightweight seeds of pioneer species but not the generally larger, heavier seeds of mature forest species (Nepstad et al. 1996; Wijdeven and Kuzee 2000). Moreover, most seeds are dispersed close to the forest edge (Wijdeven and Kuzee 2000) and under remnant forest trees (Guevara et al. 1986). Most Lower Guinea endemics are mature forest species that probably rely on larger mammals for long-range seed dispersal. In southern Cameroon, hunting is widespread and especially intensive in shifting cultivation areas (van Dijk 1999). By suppressing populations of larger vertebrates, timber exploitation, forest clearance and hunting affect dispersal of large seeded mature forest plant species (Dirzo and Miranda 1991; Maury-Lechon 1991; Bennett and Robinson 2000; Putz et al. 2000). Whether this explains the prolonged recovery of endemic species in shifting cultivation sites is, however, yet unclear.

Conclusions

We found that level of endemism, species composition and plant density are most

sensitive to shifting cultivation and selective logging. The best indicator for recovery of conservation value in our study was the level of endemism. From a biodiversity conservation standpoint, selective logging seems a better land use option than shifting cultivation. We do, however, acknowledge that sustainable forest use has socio-economic as well as biological components. Secondary forests still foster a wide range of forest plant and animal species (e.g. Lawton et al. 1998; Bennett and Robinson 2000; Putz et al. 2000). And despite the low level of endemism in especially young shifting cultivation sites, recovery of all other old growth forest characteristics was relatively fast. Therefore, secondary forests in Central Africa can contribute to biodiversity conservation, e.g. as buffer zones around forest reserves.

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